Journal of Experimental Marine Biology and Ecology 500 (2018) 34–45

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Spatiotemporal patterns of abundance and ecological requirements of a labrid's juveniles reveal conditions for establishment success and range shift capacity

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ARTICLE INFO

Keywords:
Endemic
Labridae
Range shift
Climate change
Baldchin groper
Recruitment

ABSTRACT

Distribution shifts of demersal fishes are important adaptive responses to warming oceans for species' persistence. Shifts are facilitated by factors such as adult movement and dispersal of pelagic larvae to normally cooler regions, where increasing ocean temperatures are now enhancing larval and juvenile survival. However, successful recruitment (i.e. larval settlement) at these new regions can be constrained by resource availability, specialisation (food, habitat) and ecological interactions (competition, predation). Evaluating the capacity or likelihood of a species to successfully shift or expand its range, provides information relevant to biodiversity conservation and fisheries management, and is particularly important for species with restricted ranges. *Choerodon rubescens* (Günther, 1862) is an exploited labrid endemic to ~1400 km of the west Australian coastline, encompassing 13° of latitude and a 6°C temperature gradient. This region recently experienced a rapid warming event of ~3°C, which lasted 3 months and mirrored ocean temperatures expected in the next 50 years. Following this event, high levels of recruitment of *C. rubescens* occurred towards its southern, cooler distribution limit. Juvenile abundances were surveyed in this study to evaluate: (1) the effect of elevated temperatures on recruitment success across shallow water habitats spanning the species' distribution, (2) temporal variation in recruitment success in the typically cooler, southern part of its range and (3) ecological characteristics important to recruit survival, including habitat preferences, diet and behaviour. Juvenile *C. rubescens* were significantly more abundant at the margin between reef and sand and towards the cooler southern range end. Reef margin habitat provides access to shelter from predators within the reef and to sand-associated invertebrate prey in adjacent soft sediments, where most feeding activity occurred. Juveniles were abundant (0.3 to 4 fish/40 m^2) in reef margin habitats of the southern cooler region for three consecutive years, with individuals represented by multiple cohorts, indicating suitable environmental conditions for ongoing recruitment and survival. Juveniles at this habitat were able to compete effectively with other co-occurring labrids for invertebrate prey. As oceans warm, the number of recruits arriving and surviving beyond the existing cooler range limit will be dependent on factors such as successful spawning, larval delivery and survival, and availability of reef margin habitat with associated prey; these factors will determine the successful range shift or expansion of *C. rubescens*. We present an example of how range-wide spatiotemporal ecological studies of juvenile fish can identify range shift capacity and inform management adaptive to climate change.

1. Introduction

Climate induced changes in ocean conditions are causing shifts, particularly poleward, in the distribution and abundance of many marine fishes and fishery resources (Last et al., 2011; Perry et al., 2005; Poloczanska et al., 2013). Two main mechanisms facilitate these shifts: poleward-flowing currents disperse eggs and larvae into normally cool waters (Johnson et al., 2011; Ling et al., 2009) and warming oceans

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https://doi.org/10.1016/j.jembe.2017.12.006
Received 3 April 2017; Received in revised form 12 November 2017; Accepted 1 December 2017
Available online 23 December 2017
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enable survival of newly settled recruits in these previously unsuitable environments (Booth et al., 2007; Figueira and Booth, 2010). Distributional shifts are an important "response" to localised warming, particularly for endemic species (Graham et al., 2011; Munday et al., 2008; Thomas et al., 2004). However, successful shifts may not be possible for many fish species because their survival is dependent on specific resources (e.g. food, habitat) which may not be available at locations beyond their current range (Feary et al., 2014).

Demersal fish species typically have little migration capacity as adults, with small home ranges and local-scale association with resources such as food and habitat (Bryars et al., 2012; Meyer and Holland, 2005). For these species, successful poleward shifts in their distributions require sustained larval recruitment to habitats in normally cooler environments and their establishment of populations via subsequent growth, maturation and reproduction (Crooks and Rilov, 2009). However, larval recruitment strength is highly variable in space and time, particularly in long-lived demersal species (Doherty, 1991; Jones, 1984; Russell et al., 1977; Trip et al., 2014; Williams and Sale, 1981), and these variations have subsequent effects on population size (Attrill and Power, 2002; Figueira et al., 2009; Hixon et al., 2012). Furthermore, despite warmer waters bringing larvae to novel areas, many recruits fail to survive because of the unsuitability of a range of ecological factors, including winter water temperatures, resource availability (food and habitat) and ecological interactions (competition and predation) (Caselle and Warner, 1996; Figueira et al., 2009; Hixon et al., 2012; Jones, 1984; Ross, 1986; Wilson et al., 2010).

Recruitment success (i.e. larval settlement) is typically highly variable across the geographic range of fishes, particularly for species distributed along a latitudinal gradient (Compton et al., 2007), because of the metabolic effects of a gradient in water temperatures on fish growth and survival (Lek et al., 2012; Phillips et al., 2014; Pörtner and Knust, 2007; Wakefield et al., 2017). For this reason, species tend to have thermal restrictions on their distribution, with recruitment being generally low and sporadic towards both low and high temperature extremes of their distribution (Shepherd and Brook, 2007; Zacherl et al., 2003; but see Sagarin and Gaines, 2002; Sagarin et al., 2006), where local environmental conditions are often not optimal for recruit survival (Figueira and Booth, 2010; Jones, 1984; Nantel and Gagnon, 1999).

The demersal baldchin groper *Choerodon rubescens* (Labridae) is endemic to ~1400 km of the west Australian coastline (WA) spanning a tropical to subtropical latitudinal gradient (18–24°C), where it is an important fisheries target (Fig. 1, Allen and Swainston, 1988; Edgar, 2000; Fairclough et al., 2014). It is most abundant towards the centre of its range at ~28°S and rare at both range edges (i.e. at 21 and 34°S) (Cure et al., 2018). While it undergoes pelagic dispersal during its egg and larval stages, juvenile and adults are considered to have restricted home ranges (Fairclough et al., 2011; Gardner et al., 2015; Hutchins, 2001). As with several other fish species along this coast, the distribution centroid of *C. rubescens* is predicted to shift poleward in response to gradual increases in water temperature (Cheung et al., 2012). Such future warming scenarios were recently simulated by the 2011 marine heat wave (2011 Mhw), a rapid warming event in the eastern Indian Ocean. During this event the poleward flowing Leeuwin Current (LC), which is the dominant ocean current off WA, strengthened resulting in summer water temperature anomalies of up to 3°C warmer (Feng et al., 2013; Zinke et al., 2014).

During the heatwave, fish, invertebrate and coral mortalities occurred at central latitudes along this coastline (~28°S, Abdo et al., 2012; Pearce et al., 2011). Further south along the coast, high abundances of recruits of a range of tropical and subtropical demersal species, including *C. rubescens*, were observed during the years following the 2011 Mhw in areas where they were previously in low abundance or not recorded (e.g. *Chaetodon assarius* at ~30°S, Wernberg et al., 2013, and *C. rubescens* at ~32°S, Cure et al., 2018, 2015). Although water temperatures have returned to their normal range since the 2011 Mhw, these rapid increases in recruit abundance suggest that such species are capable of undergoing poleward distribution shifts in response to warming temperatures if recruitment at southern locations is sustained by ongoing influx of recruits and/or self-recruitment. However, in order to determine range shift capacity, comparative information on recruitment patterns of such species throughout their distribution is needed, together with an assessment of the ecological requirements of newly settled recruits, to assess whether recruitment to and beyond the current cooler (southern) ends of their distribution could be sustained. Such information is crucial for developing species conservation initiatives and adapting management strategies to take into account distribution and range size changes in response to rapidly warming oceans (Poloczanska et al., 2016).

To evaluate the potential for a future range shift in *C. rubescens*, the density of juveniles and their habitat associations in shallow water lagoons where juveniles are most likely to settle (Cure et al., 2015), were first investigated across the full distribution of the species during elevated water temperatures subsequent to the 2011 Mhw. Secondly, interannual recruitment variability was examined at the cooler (southern) range end (at ~32°S) in consecutive years of elevated temperatures (2013–2015), as a proxy for the scenario of future increased water temperature conditions that may influence recruitment patterns of this species. Thirdly, to identify other specific ecological requirements of juveniles, the diet and behaviour of recruits in southern waters were determined. Data were then used to test the following hypotheses: (1) that following the 2011 Mhw, juvenile *C. rubescens* across all habitats sampled would show the previously identified pattern of higher abundance in the cooler (southern) part of the species' range rather than any other area along their distribution (Cure et al., 2018, 2015), (2) that habitats occupied by juveniles in lagoonal areas would be consistent across the species range, and (3) that as water temperatures remained higher than average, annual recruitment to the cooler (southern) end would be sustained after the high recruitment event following the 2011 Mhw (Cure et al., 2018, 2015). The detailed ecological information presented in this study will be valuable for evaluating range shift predictions and the ecological changes that may occur at receiving locations. It further highlights the need for detailed ecological data of species undergoing range shifts globally, particularly those that are exploited or occupy small ranges, such as endemics (Bates et al., 2014; Poloczanska et al., 2016).

2. Materials and methods

2.1. Study species

The baldchin groper *Choerodon rubescens* is a large subtropical protogynous wrasse (Labridae) endemic to the west coast of Australia and one of the most important recreational and commercial fisheries targets in the region (Fairclough et al., 2014). Its distribution spans a latitudinal temperature and habitat gradient from tropical coral reefs at ~21°S to temperate rocky reefs at ~34°S (Fig. 1; Allen and Swainston, 1988; Edgar, 2000; Hutchins, 2001), with abundance being highest towards the range centre and low at both range edges (Cure et al., 2018). Juveniles are common in shallow (< 3 m) protected habitats, such as lagoons (Cure et al., 2015; Fairclough, 2005; Hutchins and Swainston, 2008), and adults typically inhabit deeper and more exposed reefs up to 100 m depth (Fairclough et al., 2008). Maximum total length (L_T) and age is about 700 mm (Hutchins and Swainston, 2008) and 25 years, respectively (Fairclough et al., 2014). Juveniles attain sexual maturity as females at a minimum size of ~229 mm L_T (Fairclough, 2005). Reproduction at the centre of *C. rubescens* range occurs mostly during the austral spring to mid-summer (October to January) and juveniles settle onto the reef in summer and early autumn, i.e. December to April (Cure et al., 2015; Fairclough, 2005).

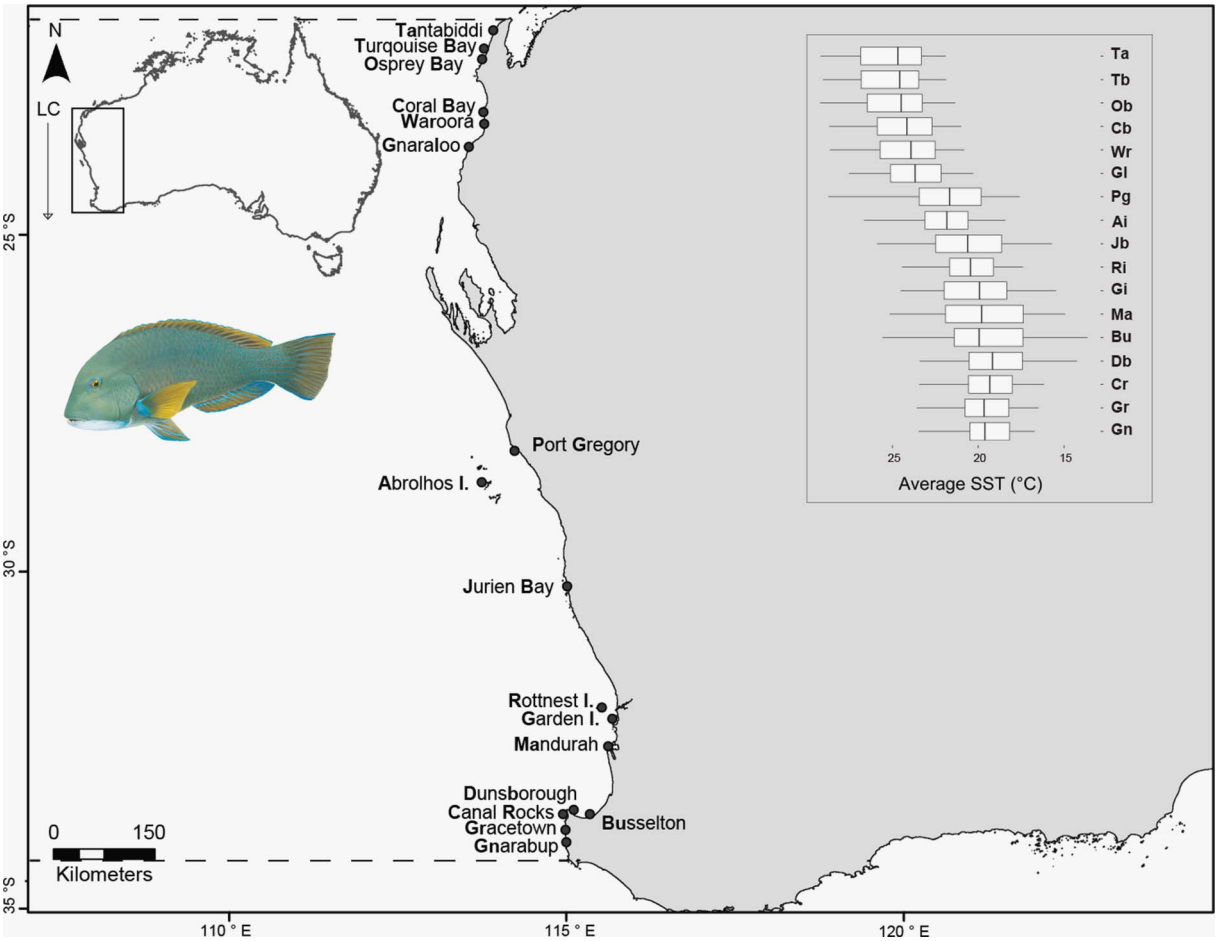

Fig. 1. Map of the study region along the west coast of Australia (WA) showing the 17 locations surveyed for juvenile *Choerodon rubescens* (< 220 mm L_T), including the entire geographic range of the species (limits between 21° and 34°S represented by dashed lines; includes all locations where the species has been recorded). Boxplot inset shows long-term (2002–2010) monthly average sea surface temperatures (SST °C) at each location (locations abbreviated in a two letter format and ordered from lowest to highest latitude); data from MODIS-AQUA satellite (Goddard Earth Sciences Data and Information Services Center, NASA); solid black lines represent median SST and box boundaries upper and lower quartiles. LC: Leeuwin Current. Baldchin groper illustration © Roger Swainston, http://www.anima.net.au.

2.2. Definition of juveniles

In this study, juveniles were defined as all fish under 220 mm L_T based on the estimated minimum size at maturity (229 mm L_T) for the species at the centre of its range (Fairclough, 2005). Growth patterns along northern and central locations of *C. rubescens* range (i.e. Shark Bay and Abrolhos Islands) indicate that juveniles observed during this study would comprise up to three age classes, i.e. 0+, 1+ and 2+ (Fairclough, 2005; Nardi et al., 2006). As range-wide surveys in this study were conducted during 2013 (see Section 2.4 below), the combined abundance of fish under 220 mm L_T would most likely consist of juveniles recruited during the summer/autumn recruitment seasons of 2010/11, 2011/12 and 2012/13. Similarly, temporal surveys conducted during 2013 to 2015 (see Section 2.4) that recorded fish of 40 to 220 mm L_T would likely indicate recruitment events during the year surveyed and the previous two years. Specific ages of juvenile fish at southern locations where temporal surveys were conducted, were further estimated from fish collections in order to better understand recruitment patterns in *C. rubescens* and validate juvenile ages in this region where juvenile size-at-age data are not available (see Section 2.3).

2.3. Age estimation of juvenile fishes

In order to better identify recruitment periods at sites in the cooler (southern) end of *C. rubescens* range, post-settlement ages of juveniles collected haphazardly using hand-spear while free-diving in shallow water lagoons (< 3 m) at Garden Island (32.12°S, 115.66°E) and Mandurah (32.60°S, 115.64°E) between January and April 2013, were calculated. Settlement marks were evident in some of the otoliths examined, but we were not able to determine pelagic larval duration in all individuals; for this reason, post-settlement ages were calculated. A total of 60 juvenile *C. rubescens* of 45 to 161 mm L_T were collected haphazardly (Garden Island, $n = 41$ and Mandurah, $n = 19$), representing the full size range of individuals observed. Each captured fish was measured to the nearest mm L_T, and its sagittal otoliths removed, cleaned in ethanol and stored dry. In order to be able to read daily growth rings, otoliths were ground to the central core and polished by hand with lapping film (0.3–3 μm) following Choat et al. (2003). Each sectioned otolith was mounted on a slide, covered with clear Crystalbond thermoplastic cement (Aremco) for reading and placed under a compound microscope with transmitted light and 40× magnification. Individual post-settlement ages (days) were estimated by counting daily opaque growth zones following the settlement band clearly displayed on each otolith (Wilson and Mccormick, 1999). Daily ring formation has previously been validated for juvenile labrids of the same genus (*Choerodon schoenleinii*; Yamada et al., 2009). Blind reads of daily increments were performed twice by ECT, and validated by the first author who is an experienced otolith reader. Each read was done at least one week apart without knowledge of the length of the fish or its date of capture. If the error between the first two reads was > 10%, a third blind read was conducted by the senior author following the same

guidelines as the first reader. An average of the two closest counts was used as the estimate for age. Settlement dates were also calculated for each individual fish collected based on capture date and estimated post-settlement age. These ageing data allowed us to determine whether our sampling captured one or more years of recruitment.

2.4. Density surveys

We surveyed juvenile *C. rubescens* in shallow (< 3 m) protected lagoonal environments at 17 locations spanning its full geographic range between April and November 2013 (~1400 km, Fig. 1), following the 2012/13 recruitment season for this species. These surveys include data presented in Cure et al. (2015); in this study, we expand these initial surveys both geographically (across the species range) and temporally (across 3 years). At the geographic range level, each location was surveyed once during April to November 2013, given the logistic difficulties associated with sampling across a large latitudinal gradient in a remote coastline. At each location, we surveyed three broad habitat types where *C. rubescens* is known to occur: (1) 'reef' habitat corresponded to areas of continuous reef (coral or rocky), (2) 'reef margin' represented the edge between reef and sand and (3) 'macrophyte beds' consisted of seagrass or macroalgal beds < 1 km from the reef margin. Habitat types surveyed at each location were < 1 km apart.

The numbers of juvenile *C. rubescens* were recorded during snorkel based underwater visual census (UVC) along 12 replicate transects (10 × 4 m) laid haphazardly in each habitat at each location. UVC has been previously used successfully to survey juveniles of *Choerodon* species and distinguish their density among habitats (Fairclough et al., 2008). The L_T of each fish observed was estimated to the nearest 10 mm by the first author, who trained in fish length estimation following Bell et al. (1985). The precision of UVC length estimates was further tested during fish collections for age and diet assessments (see Sections 2.3 and 2.6), via estimation of the L_T of each fish prior to harvesting and posterior comparison with its L_T measured in the laboratory. While swimming back along each transect at 0.5 m increments, the point intercept method was used to record habitat characteristics according to 12 benthic categories (sand, rubble, brown foliose algae, turfing algae, brown canopy forming algae, red algae, green algae, kelp, seagrass, hard coral, soft coral and limestone). The number of points per benthic category was later converted to percent cover.

To evaluate recruitment variation over time at the cooler (southern) end of *C. rubescens* distribution, we surveyed three locations (Garden Island, Rottnest Island and Mandurah, at ~32°S), where a high recruitment event was previously detected (Cure et al., 2015). Surveys were conducted towards the end of the recruitment seasons of 2012/13 (data also in Cure et al., 2015), 2013/14 and 2014/15 (during January to May). At each location, between one and four sites were surveyed (Garden Island $n = 1$, Rottnest Island $n = 4$, Mandurah $n = 1$), with the same number of sites surveyed once during each of the three recruitment seasons at each location. At each site, the number of juveniles was recorded on 12 replicate 10 × 4 m transects in each of the three habitat types where *C. rubescens* is known to occur (reef, reef margin and macrophyte beds). The L_T of each individual was also estimated to the nearest 10 mm and recorded.

Average monthly sea surface temperatures (SST, °C) from 2002 to 2015 were obtained for each location surveyed via MODIS AQUA satellite derived data (at 4 km resolution), available from the Goddard Earth Sciences Data and Information Services Center, NASA. Long term decadal (2002 – 2010) and annual average SSTs during and after the 2011 Mhw for austral winter (June to August) and summer (December to February) seasons were then calculated from these data.

2.5. Behavioural observations

Between January and April 2013, in situ behaviours of 26 haphazardly selected juvenile *C. rubescens* (est. L_T: 40–180 mm, mean ± SE: 115 ± 7 mm) were recorded at Garden Island (32°S, 115°E) (Fig. 1) in 'reef margin' habitat at 1–3 m depth, where the probability of juvenile encounters was high. Preliminary observations identified the main behaviours displayed by *C. rubescens* juveniles as (1) searching (swimming along the substrate until stopping at a feeding site), (2) feeding (foraging for food while stationary in a particular area), and (3) chasing (an interaction with either conspecifics or other fish species, which resulted in chasing or being chased away from a particular habitat). For each individual, one minute of adaptation to observer presence was allowed before recording behaviours for 3 min (Shepherd, 2005). The total time engaged in each of the three identified behaviours during each 3 min observation period was recorded and converted to a percentage. If a chosen juvenile exhibited a flight response or showed evidence of disturbance (e.g. sheltering), the observation was aborted. The number of bites and pectoral fin fans (PFFs) during feeding were recorded. PFFs were distinctive of feeding activity in juvenile *C. rubescens* and consisted of the use of pectoral fins (individually or alternating) to fan soft sediments and uncover buried prey (Wainwright and Bellwood, 2002). General benthic habitat in the location where each behaviour occurred was recorded according to 4 broad categories (sand, rubble, macroalgae and seagrass).

2.6. Dietary analyses

To determine the diet of juvenile *C. rubescens*, 55 individuals (45 to161 mm L_T) were collected at Garden Island (32°S, 115°E) (Fig. 1) between January and April 2013 by hand-spear. Fish were immediately euthanized in an ice slurry. In the laboratory, the L_T of each individual was measured to the nearest mm. Its whole gut was removed and preserved in 70% ethanol for later examination of foregut contents (first third of the gut where items are relatively undigested). Laboratory procedures for dietary analyses followed Lek et al. (2011). The fullness of each foregut was scored from 1 to 10, with 1 being empty and 10 being fully distended. All dietary items were then identified to the lowest possible taxonomic level under a dissecting microscope and using relevant taxonomic literature (Edgar, 2000; Grove, 2011; Jones and Morgan, 2002; Wells and Bryce, 1986; Wilson, 2002). Following identification of major prey items the volumetric contribution (%V) of each dietary item to the total gut contents of each fish was visually estimated using a grid following methods in Hyslop (1980), and the frequency of occurrence (%F) of each item calculated. The volumetric contributions of the different dietary items were then grouped into ten major dietary categories following Lek et al. (2011).

2.7. Statistical analyses

We used univariate permutational analyses of variance (PERMANOVA) to test for differences in (1) the density of juvenile *C. rubescens* across the geographic range of the species, and (2) spatio-temporal variation of juvenile density at the three locations at ~32°S. In each case, PERMANOVA was conducted on a Euclidean distance resemblance matrix constructed from untransformed juvenile *C. rubescens* densities (Anderson, 2001; Anderson and Millar, 2004). Analyses were run with 9999 permutations, type III sums of squares, and permutation of residuals under a reduced model, using the PRIMER v 6.1.15 software (Anderson et al., 2008; Clarke and Gorley, 2006). To test for significant range-wide spatial variation in juvenile density we used a two-way crossed design with location (17 levels; random) and habitat (3 levels; fixed) as factors. For assessment of significant spatiotemporal variation in juvenile density towards the cooler end, we used a three-way crossed design with year (3 levels; fixed), location (3 levels; random) and habitat (3 levels; fixed) as factors. Year was kept as a fixed effect because of the limitations associated with making inferences about interannual variation from a low number of years surveyed (Anderson and Millar, 2004). Our results are thus only indicative

of differences between the three years sampled. Pair-wise PERMANOVA tests were conducted on fixed factors for both designs to assess the key factors behind any significant interaction terms and identify homogenous groups at the level of interest.

Differences in the composition of benthic habitats used by *C. rubescens* across its range were explored by characterization of the multivariate data using principal components analysis (PCA) and overlaid vectors representing the most important benthic categories (correlations > 0.20 with PCA axes). Benthic composition PCA was based on a Euclidean distance matrix generated from square root transformed percent cover data at the transect level.

Behavioural time budgets for individual *C. rubescens*, i.e. the time spent undertaking each behaviour during a 3 min observation, and their relationships to benthic habitat where each behaviour occurred (4 levels: sand, rubble, macroalgae, seagrass) were also assessed via univariate PERMANOVA (% of total time for each individual) using a Euclidean distance resemblance matrix constructed with untransformed data. A two-way design with fixed factors behaviour (3 levels) and benthos (4 levels) was used. Pair-wise post hoc PERMANOVA was then used to test for homogeneity of behaviours observed according to benthos.

3. Results

3.1. Range-wide patterns in juvenile abundance and habitat associations

A total of 183 juvenile *C. rubescens* were recorded at seven of the 17 locations surveyed (Waroora, Port Gregory, Abrolhos, Jurien Bay, Rottnest Island, Garden Island and Mandurah; Fig. 1, 2), while none were observed at the most northern (Tantabiddi to Coral Bay, i.e. < 23°S) and southern (Dunsborough to Gnarabup, i.e. > 33°S) locations surveyed (see Figs. 1, 2). Seventy nine per cent of individuals occurred at some of the most southern locations surveyed, i.e. Rottnest Island (n = 52 juvenile fish), Garden Island (n = 29) and Mandurah (n = 63), and the greatest mean densities occurred at the latter two (Fig. 2). PERMANOVA detected a significant difference in the mean density of juvenile *C. rubescens* among the 17 locations and three habitats surveyed and a significant interaction between the two factors (Table 1). Observed variations in density across *C. rubescens* distribution were dependent on the habitat surveyed (Fig. 2). Pairwise PERMANOVA demonstrated that juvenile density was consistently higher in 'reef margin' habitat, except at the Abrolhos Islands, where most juveniles were recorded in 'macrophyte beds' and mean density was low (Fig. 2). In 'reef margin' habitat, density was greater in locations at ~32°S, i.e. Rottnest Island, Garden Island and Mandurah, towards the cooler (southern) range margin. However, geographic differences in juvenile density within the other habitats surveyed were less pronounced (Fig. 2).

3.2. Growth of juvenile Choerodon rubescens and settlement date estimates

Estimated post-settlement ages for the 60 juvenile *C. rubescens* collected (45 to 161 mm L_T) indicated that they were all less than a year old (0 + fish; 72 to 283 days), considering that the average pelagic larval duration for the species is ~23 days (K. Cure, unpublished data). Ageing results therefore show that based on length frequencies, the temporal juvenile surveys conducted towards the cooler (southern) range edge consisted mostly of 0 + fish, and therefore fish that recruited during 2012/13, 2013/14 and 2014/15 (Fig. 3). Calculation of specific settlement dates based on capture date and estimated post-settlement ages, indicated that two major recruitment events occurred during 2012/13: one during winter representing 53% of juveniles surveyed (June to August 2012, n = 32), and another one during summer representing 32% (December 2012 to February 2013, n = 19); the remaining juvenile fish recruited sporadically during other times of the year (n = 9, 15%). Growth of *C. rubescens* juveniles at the two sites along the southern end of the species' range (32°S) was linear during the first year of life (L_T = 0.4121 x Age + 27.048, where age is in days; R^2 = 0.81) (Fig. 3).

3.3. Spatiotemporal patterns in juvenile abundance and size towards the cooler range edge

We found considerable spatiotemporal variation in density of juveniles at the three locations surveyed towards the cooler (southern) range edge (Table 1b, Fig. 4). There was a significant interaction between the effects of year, location and habitat on juvenile density, indicating that the effects of year and habitat were not equal across all locations sampled (Table 1b, Fig. 4). Juvenile density was always highest in the 'reef margin' habitat for all locations and this pattern held through time (Fig. 4). Mandurah showed higher juvenile density than both Garden Island and Rottnest Island during 2013, but juveniles were absent at this location during 2014. For Garden and Rottnest Islands, there was relatively little variation in fish density between years. Average SST at the three locations remained relatively high with respect to long-term averages during the summer of 2012/13 and 2013/14, and was slightly lower during 2014/15. Average winter temperature at these locations was 0.62 °C higher than the long-term average during 2012, but returned to long-term averages from 2013 to 2015 (Table 2). Length frequency distributions at all sites indicated that during each of the three years surveyed there was recruitment of *C. rubescens* juveniles, except during 2014 at Mandurah, when no recruits were recorded (Fig. 5).

3.4. Benthic characteristics of habitats surveyed

Each habitat surveyed across the latitudinal gradient was characterized by a different benthic composition (Fig. 6). Benthic components with the greatest influence on habitat separation along the PCA axes were: (1) seagrass, which was characteristic of 'macrophyte beds', (2) sand, brown canopy forming algae and rubble, which were positively associated with the 'reef margin', and (3) hard coral which drove separation of the 'reef' habitat from the other habitat types. The first two principal component axes for this multivariate dataset accounted for 54.2% of habitat variation, most of which was due to separation of 'macrophyte beds' from the other two habitats surveyed.

3.5. Behaviour and diet

Juvenile time budgets were dominated by feeding behaviour. Fish spent the majority of each 3 min observation either feeding in a single area (~63%, 113 ± 13 s) or searching for food (~34%, 62 ± 12 s) (Fig.7A). Benthos used by juvenile fish in order of importance were: sand (35% of the 3 min observation), rubble (25%), macroalgae (27%) and seagrass (13%) (Fig. 7B). There was a significant interaction between behaviour and habitat (PERMANOVA, $F_{(6300)}$, p = 0.04, see Supplementary material Appendix 1). At rubble and seagrass, time was evenly allocated to the three behaviours recorded (feeding, searching and chasing) (Fig. 7B). However, over sand substrates, juveniles spent 80% of the time feeding and searching, with time equally allocated to both behaviours (Fig. 7B). Feeding occurred mainly over sand (52%), followed by rubble (38%) and macroalgae (10%). When juveniles were feeding, bite rate was on average 2.44 bites min^{-1}. Pectoral fin fans (PFFs), which occurred over both sand and rubble, were more common than bites (3.64 per min^{-1}). Feeding typically followed a sequence which consisted of: (1) using PFFs to dig a hole, and (2) using tusklike teeth to either dig out prey buried in soft sediments, or capture prey under pieces of rubble which were removed and tossed to the side (imagery provided in Supplementary material Appendix 2). Chasing, the least common activity (Fig. 7A), was recorded almost exclusively at these feeding holes, with the observed fish chasing either other juvenile *C. rubescens* or other wrasses away from their feeding holes (i.e. *Coris*

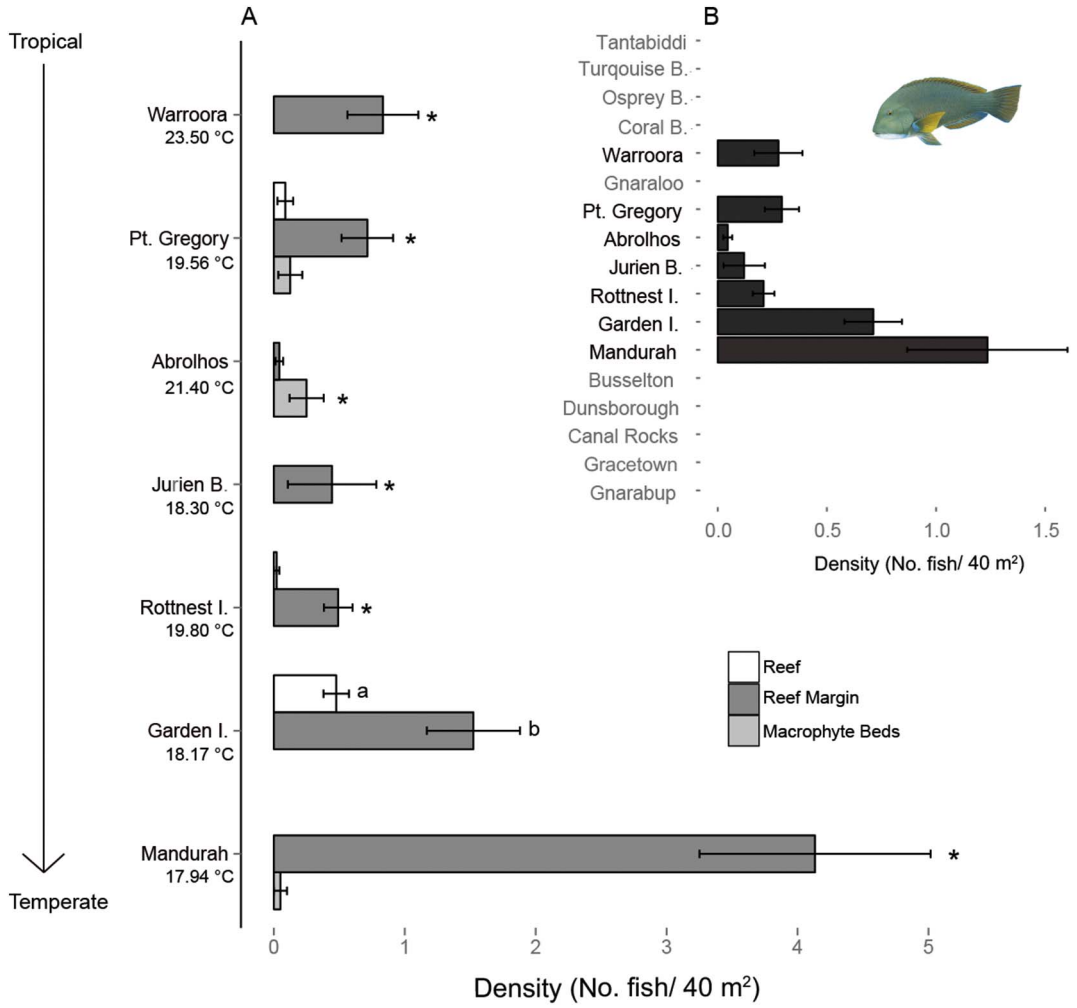

Fig. 2. Mean density (No. fish/40 m^2 ± SE) of *Choerodon rubescens* juveniles (< 220 mm L_T) at the 17 locations surveyed along the entire geographic range of the species: (A) density at the habitat level (reef, reef margin and macrophyte beds) for the seven locations where juveniles were present, and (B) overall density per location. Surveys were undertaken between March and November 2013, once at each location. Temperatures below each location label correspond to mean winter sea surface temperature (SST, °C) for 2011–2013 from MODIS-AQUA satellite data. At each location, density was estimated on 36 belt transects (10 x 4 m), 12 by habitat. Asterisks represent significant differences between habitats at each location ($p < 0.05$), and lower case letters represent homogenous groups from post-hoc tests ($p < 0.05$). Baldchin groper illustration © Roger Swainston, http://www.anima.net.au.

Table 1
PERMANOVA test results describing spatial variation of *Choerodon rubescens* juvenile densities (< 220 mm L_T), across (a) the species' geographic range along the west coast of Australia, and (b) spatiotemporal variation of juvenile density at the three most southern locations where juveniles were found (Rottnest Island, Garden Island, Mandurah).

Source	df	SS	Pseudo-F	p
(a)				
Location	16	87.24	12.52	**0.001**[a]
Habitat	2	53.86	61.83	**0.001**[a]
Lo × Hab	27	166.39	14.15	**0.002**[a]
Error	566	318.41		
(b)				
Year	2	30.34	2.39	0.174
Location	2	14.26	10.07	**0.001**[a]
Habitat	2	148.72	10.76	**0.035**[a]
Ye × Lo	4	26.35	9.30	**0.001**[a]
Ye × Hab	4	46.57	1.73	0.220
Lo × Hab	4	28.90	10.19	**0.001**[a]
Ye × Lo × Hab	8	56.64	9.99	**0.001**[a]
Error	695	384.65		

[a] Represents a significant effect.

auricularis). Focal *C. rubescens* were only chased away during interactions with *Notolabrus parilus*, which occurred over macroalgae.

The mean volumetric contributions to diet of *C. rubescens* juveniles were dominated by gastropods (28.62%), large crustaceans (24.63%; mainly penaeids, paguroids and brachyuran crabs) and bivalves (20.21%) (Fig. 8, Supplementary material Appendix 3). Of the 36 identified prey items, half were soft sediment associated prey (Edgar, 2000; Grove, 2011; Jones and Morgan, 2002; Wells and Bryce, 1986; Wilson, 2002), including polychaetes, sand anemones, brachyuran crabs (Majidae, Portunidae), Cumacea and gastropods in the families Cerithidae, Rissoidae and Naticidae. The volumetric contribution of bivalves and small crustaceans was greater in juveniles with L_T < 100 mm than juveniles with L_T > 100 mm, while that of large crustaceans and echinoids was greater in juveniles > 100 mm L_T (see Supplementary material Appendix 3). Larger juveniles also had greater foregut fullness (mean 5.1 vs 3.4, Supplementary material Appendix 3).

4. Discussion

Our surveys across multiple shallow-water habitats with a juvenile-focused underwater visual census (UVC) technique showed that two years after a marine heatwave event during the summer of 2010/11, significantly greater densities of juvenile fish were found at cooler (southern) rather than warmer (central/northern) parts of *C. rubescens*

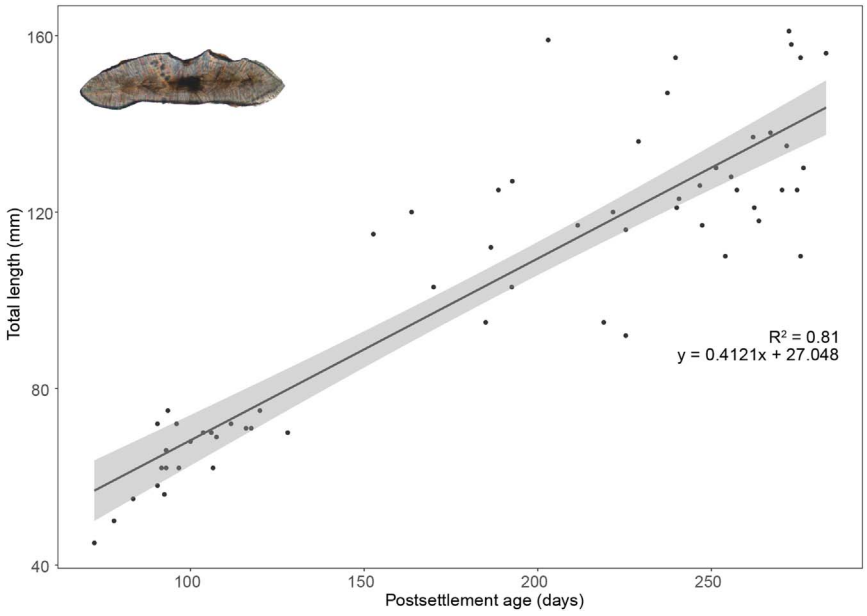

Fig. 3. Size at age plots with fitted linear regressions for *Choerodon rubescens* juveniles (< 220 mm L_T, n = 60) collected via hand-spear at two sampling localities towards the cooler southern range end (Garden Island and Mandurah, 32°S). Grey bands represent ± 2*SE of the model fit estimate. Age was determined by counting daily rings on otolith sections, image represents otolith section seen at 40 × magnification and is not to scale.

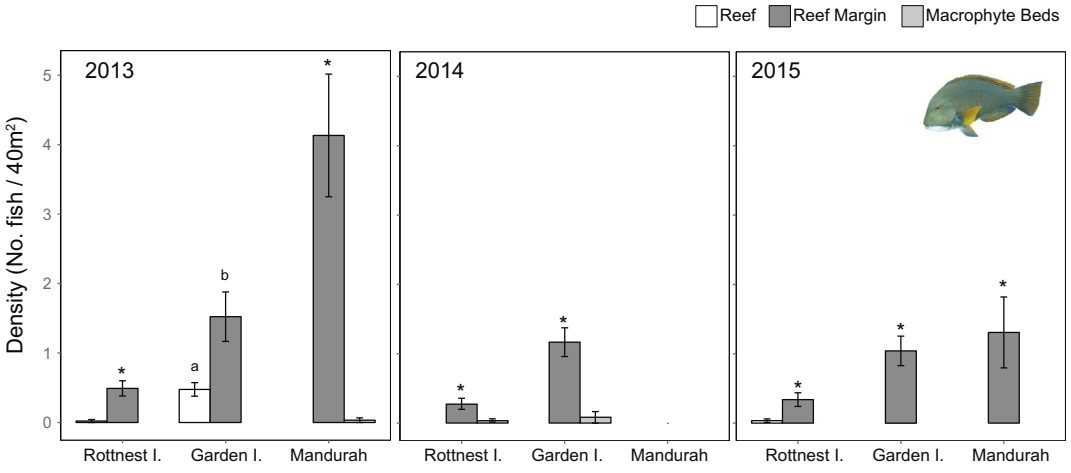

Fig. 4. Mean density (No. fish/40 m^2 ± SE) of *Choerodon rubescens* juveniles (< 220 mm L_T), in reef, reef margin and macrophyte bed habitats at the three most southern locations where juveniles were found (Rottnest Island, Garden Island and Mandurah) between 2013 and 2015 (note each year represents a summer/autumn recruitment season so that 2013 would represent Dec 2012/May 2013). Densities were estimated yearly at between one and seven sites across the three locations, on 12 belt transects (10 x 4 m) per habitat wherever possible. Asterisks represent significant differences detected between habitats at each location ($p < 0.05$), and lower case letters represent homogenous groups from post-hoc tests ($p < 0.05$). Data for 2013 are also presented in Cure et al. (2015). Baldchin groper illustration © Roger Swainston, http://www.anima.net.au.

distribution along the west coast of Australia. These results confirm observations from diver-operated stereo-video surveys in deeper waters suggesting that as a result of warmer temperatures during this heatwave event (up to 3°C above long-term average; Hobday and Lough, 2011; Benthuysen et al., 2014; Pearce and Feng, 2013), juvenile distribution has shifted southward with respect to that of adults, with this pattern indicating the potential for the species' distribution to change as environmental change occurs (Cure et al., 2018). Recruitment in cooler parts of *C. rubescens* range continued for a further two years (summer/autumn of 2013/14–2014/15), indicating that suitable environmental conditions existed for ongoing recruitment and survival of *C. rubescens* towards and perhaps beyond, its cooler range edge.

With a stronger Leeuwin Current flow associated with the 2011 Mhw, *C. rubescens* larvae may have been carried into normally cooler parts of their range in greater abundances (Cure et al., 2017; de Lestang et al., 2014; Feng et al., 2013), and their growth and survival at these locations enhanced by warmer ocean temperatures particularly during winter (Figueira et al., 2009; Figueira and Booth, 2010) when we found evidence for recruitment in this study. Furthermore, warmer ocean temperatures towards the cooler (southern) end of *C. rubescens*

Table 2
Average sea surface temperatures (mean ± SE, °C) during winter (wSST) and summer (sSST) at the three most southern locations where juvenile *C. rubescens* were found (Rottnest Island, Garden Island and Mandurah). Included are long-term temperatures (2002–2010), temperatures relative to the 2011 marine heat wave event (2010/11 and 2011/12) and temperatures during time periods relative to juvenile *C. rubescens* temporal surveys and the recruitment events they most likely represent (from 2012/13 to 2014/15).

	2002–2010	2010/11	2011/12	2012/13	2013/14	2014/15
sSST	21.54 °C ± 0.18	22.84 ± 0.40	22.89 ± 0.40	22.73 °C ± 0.30	22.29 °C ± 0.44	21.96 ± 0.72
wSST	18.44 °C ± 0.18	18.81 ± 0.31	19.06 ± 0.29	18.45 °C ± 0.24	18.44 °C ± 0.54	18.30 ± 0.25

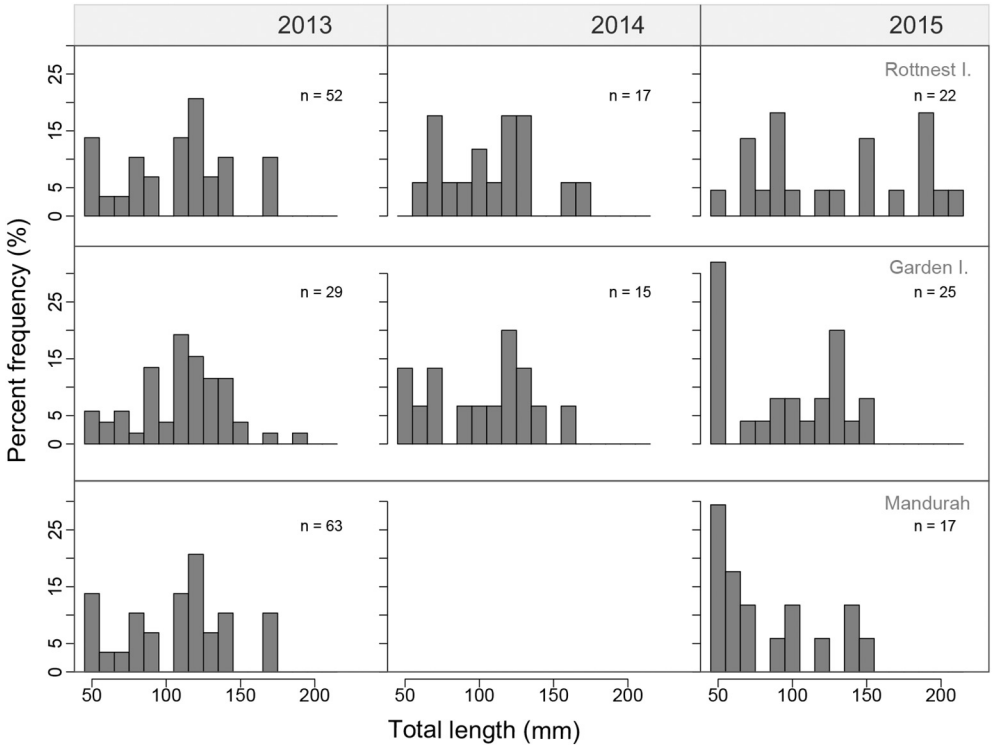

Fig. 5. Length-frequency distributions of *Choerodon rubescens* juveniles (< 220 mm L_T) at the three most southern locations where juveniles were found: Rottnest Island (top box), Garden Island (central box) and Mandurah (bottom box) between 2013 and 2015. Data are presented as percent relative frequency (%) per 10 mm length bins. *n* = total number of fish recorded during UVC surveys.

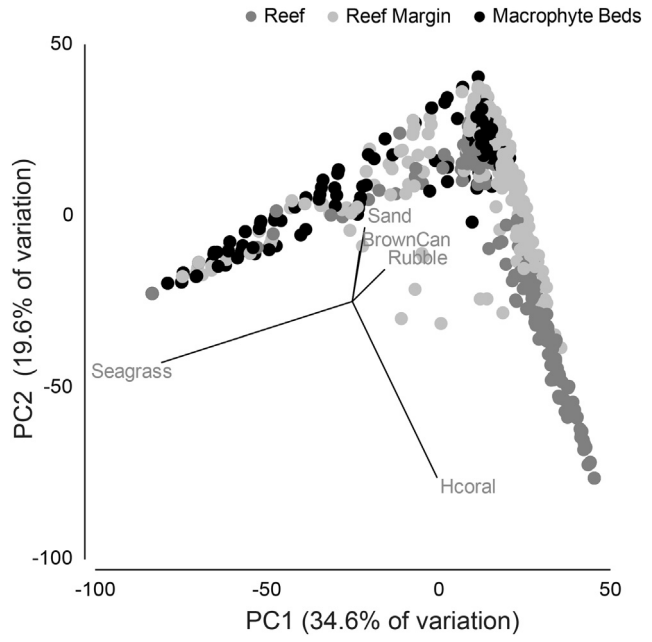

Fig. 6. Principal Coordinate Analysis (PCA) showing differences in benthic composition along the three habitats sampled (reef, reef margin and macrophyte beds) at the 17 locations sampled across the geographic range of *Choerodon rubescens*. Vectors represent the relationship of benthic variables recorded (% cover, 12 categories) with each PC axis; only variables with correlations > 0.20 are shown (seagrass, sand, brown canopy forming algae, rubble and hard coral).

distribution could have increased spawning success of local adult populations and/or survival of associated recruits. In contrast, at the warmer end of the species' range, larvae may have been exported via stronger southward current flow (Feng et al., 2013), and local recruitment may have been lacking because warmer temperatures may have exceeded thermal tolerance limits, having negative effects on spawning success, larval survival and/or growth (Berumen et al., 2011; Munday et al., 2008; Takahashi et al., 2012). These observed alterations to recruitment patterns are consistent with long-term predictions of a southward shift (approximately 78 km by 2055) in the range centroid of *C. rubescens* in response to warming oceans (Cheung et al., 2012), and have been previously suggested from a range-wide assessment of length-frequency distributions in the species (Cure et al., 2018).

Along with oceanographic influences, the types of habitat and food resources available at the cooler margin of *C. rubescens*' range may affect recruitment success, growth and survival of individuals. During this study, juveniles were common primarily at the margin between reef and sand and were observed to feed on associated soft sediment invertebrate prey at the cooler (southern) range margin where a high recruitment event was recorded (see also Cure et al., 2015). The reef habitat provides refuge from predators (Hixon and Beets, 1993), while sandy substrates support the invertebrate prey *C. rubescens* feeds on (Hobson and Chess, 1986; Langlois et al., 2005; Lindquist et al., 1994). Association of juveniles with reef margin habitats was consistent in locations where this species was observed throughout its range during 2013 and over time (2013–2015) at the southern locations surveyed. Presence of protected lagoonal reef margin with adjacent large sand patches therefore appears crucial to colonization of new habitats by this species beyond its present range. This type of habitat is sparse and occurs at isolated locations along shallow waters in the Capes region (150 km south of Mandurah; Sanderson et al., 2000), which currently represents the cooler (southern) margin of *C. rubescens* range. In this region, reef substrate starts to change gradually from limestone to granite, with associated fish assemblages also changing significantly (Harman et al., 2003).

The sparsity of settlement habitat in the Capes region (Sanderson et al., 2000) constitutes a potential reason for the lack of juvenile observations in this area subsequent to the heatwave event and may be an important limitation for range expansion capacity in the species. Like many other labrids, *C. rubescens* is a generalist invertivore, with its juveniles consuming a range of sand dwelling prey (Lek, 2004; Lek et al., 2011; Shepherd, 2005). Thus, juveniles are unlikely to be restricted by the availability of food resources at the southern margin of *C. rubescens* distribution, even if local prey species differ from those

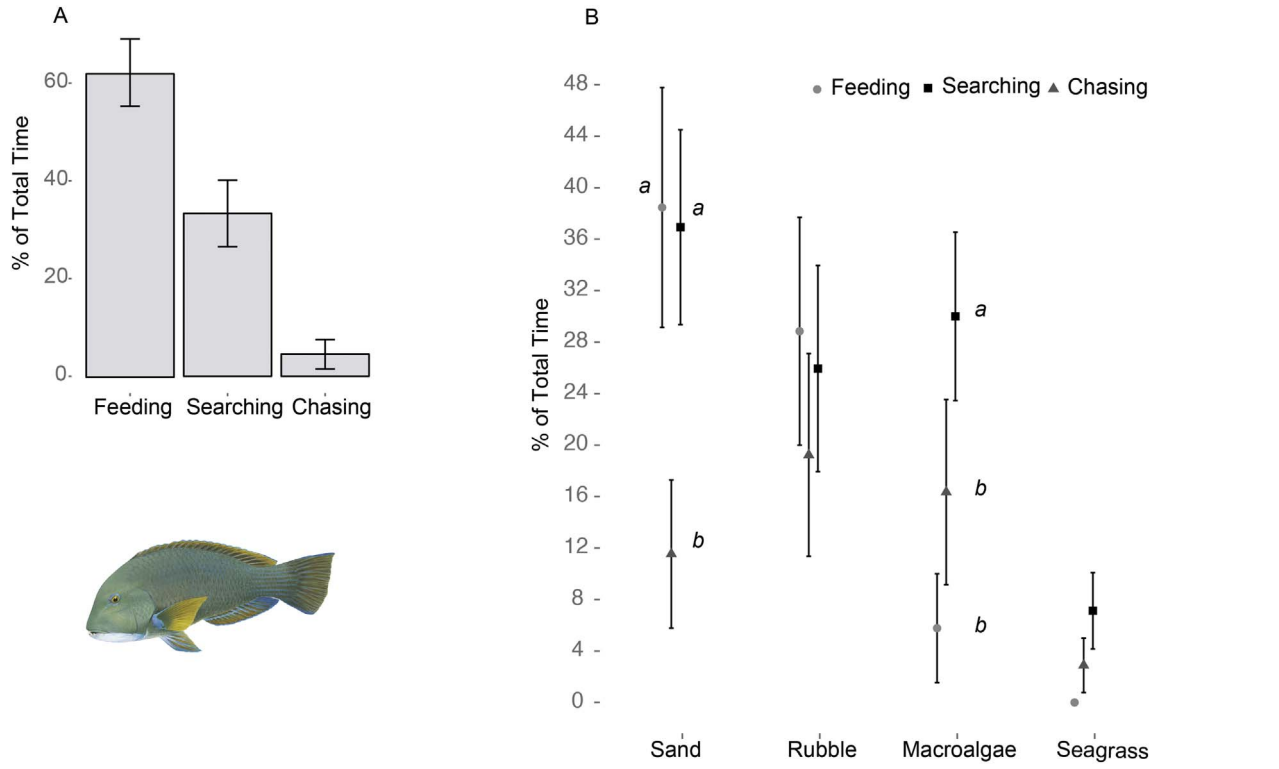

Fig. 7. Time budget summaries for the three behaviours (feeding, searching and chasing) exhibited by juvenile *Choerodon rubescens* (40–180 mm L_T, $n = 26$) at the reef margin habitat in Garden Island, Western Australia. Shown are: (A) mean percentage of time (± SE) allocated to the three behaviours recorded in order of importance, and (B) mean percentage of time (± SE) allocated to each behaviour recorded according to benthos (sand, rubble, macroalgae and seagrass). Lower case letters represent homogenous groups from post-hoc tests at the benthos level (PERMANOVA, $F_{(6300)}$, $p < 0.05$, see Supplementary material Appendix 1). Baldchin groper illustration © Roger Swainston, http://www.anima.net.au.

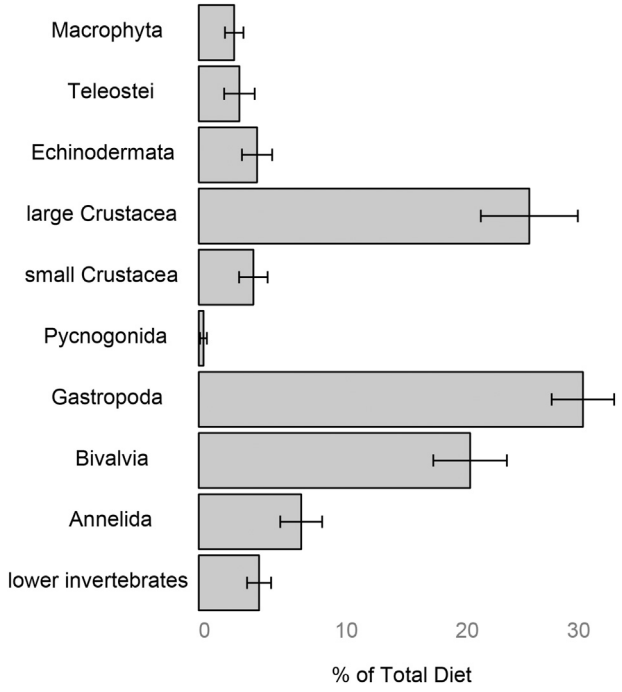

Fig. 8. Mean percentage volumetric contributions of the ten dietary categories to the diets of juvenile *Choerodon rubescens* collected at Garden Island, Western Australia (45–161 mm L_T, $n = 55$).

throughout the rest of the species' range, or invertebrate prey composition changes as a result of environmental change (Feary et al., 2014). Behavioural data indicated that *C. rubescens* can chase away competitors from its feeding sites despite this behaviour being a minor component of juvenile time budgets, indicating that the species can compete for invertebrate prey with other co-occurring subtropical and temperate labrid species (e.g. *Achoerodus gouldii*, *Bodianus frenchii*, *Notolabrus parilus*, *Coris auricularis*) on the reef margin habitat, despite likely similarities in their diet (Lek et al., 2011; Platell et al., 2010; Shepherd, 2005). The extent of such competition for food would also be influenced by the partitioning of resources, such as habitat, by the early life history stages of such morphologically similar species. This would be reduced by the fact that small juveniles of some of those species occupy different habitats to juvenile *C. rubescens*, such as reef caves/ledges (e.g. Fairclough, 2016).

In summary, our analysis of range-wide juvenile abundance patterns and ecological requirements of *C. rubescens* provides support for the ability of this species to adapt to warming ocean temperatures, with the potential for the centroid of its distribution to shift southwards (Cheung et al., 2012). We found that juvenile recruitment in cooler parts of *C. rubescens* range has been sustained for at least three years (recruitment seasons of 2012/13, 2013/14 and 2014/15) despite some variation between locations and years. Sustained recruitment of *C. rubescens* juveniles was presumably facilitated by warmer ocean temperatures, their generalist food requirements, and the availability of their preferred reef margin habitats. However, we identified several possible limitations to a predicted distributional shift, including changes to larval dispersal and delivery caused by changing oceanographic conditions, and the reduced availability of nearby shallow water protected lagoons with suitable recruitment habitat beyond the existing cooler margin of the species' distribution. The varying effects of such factors highlight the need for continued monitoring to determine whether the predicted range shift eventuates, and points towards the uncertainty of the distributional response of individual species despite a seemingly global generalization of poleward range shifts (Perry et al., 2005; Poloczanska et al., 2013). Continued monitoring would also be beneficial in identifying what would be considered normal interannual recruitment

strength variation and what would be an unusually high or low recruitment, which may signal a change in the patterns of recruitment across the species' range.

WA is a global endemic hotspot for marine fishes and marine organisms in general (Allen, 2008; Roberts et al., 2002). Models have predicted that, as water temperatures rise off the WA coast, the distribution of endemic fishes will shift poleward (Cheung et al., 2012). However, these predictions require empirical testing because ecological interactions and availability of resources will influence predicted range shifts. This study of *C. rubescens* represents an empirical test of these predictions during a period of elevated ocean temperatures that mirrored predicted temperatures of 2070 (Hobday and Lough, 2011). It thus serves as an example of how this and other important commercially and recreationally fished species with similar distributions (e.g. *Epinephelides armatus*, *Glaucosoma hebraicum*) may be influenced by either rapid warming or gradual long-term temperature increases. The considerable changes to species' distributions that are occurring as a result of changing climate and their direct ecological impacts, including altered food chains and changes in the composition of habitat forming species (Bennett et al., 2015; Lloyd et al., 2012; Vergés et al., 2014), call for effective assessments of such changes. Such information would be beneficial to management agencies with key performance indicators associated with biodiversity and/or fisheries production. In the case of *C. rubescens* for example, extension into novel habitats has the potential to alter habitat-forming algae via increased predation on mollusks and urchins, which are the main herbivores on subtropical and temperate ecosystems (Poore et al., 2012). This study highlights the importance of range-wide ecological assessments of juvenile fishes in the field in order to evaluate models predicting distributional change (Cheung et al., 2012; Thomas et al., 2004), as well as the uncertainty and complexities surrounding these predictions.

Acknowledgements

We thank E. Lek for advice on diet assessment and A. Brearley for assistance with prey identification. K. Lema, S. Moyle and A. Ash assisted with fish surveys. C. Rousseaux from NASA, assisted with SST data access. This work was conducted under approval from: WA Department of Fisheries Exemption No. 2298, Rottnest Island Authority Permits No. 2013/183879 and No. 2015/234025, Animal Ethics PUA Ref: F1 1043.

Funding

This work was supported by the School of Plant Biology, University of Western Australia, and a Holsworth Wildlife Research Endowment to KC.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2017.12.006.

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